# FOREST OPENINGS AND THE DISTRIBUTION OF UNDERSTORY BIRDS IN A PUERTO RICAN RAINFOREST

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ABSTRACT.—From October 1983 through September 1984, 19 two-day mist-net censuses were conducted in a tabonuco (*Dacroydes excelsa*) forest in Puerto Rico to examine the species richness and composition of the understory avifauna in small treefall gaps, a larger powerline opening, and forest understory. We captured 531 birds representing 17 species. Although numbers of species captured in the three habitats were similar, numbers of captures differed among habitats. Of the 12 species with adequate sample size, 6 were captured significantly more often in at least one habitat of a pair (gap-forest, gap-powerline, powerline-forest). Analysis of all nets by Bray-Curtis ordination indicates that although gap and forest assemblages are distinct, both overlap with the powerline opening assemblage. Treefall gaps were probably too small and rare to support gap specialist birds, and differences between gap and forest assemblages can be attributed to the presence of canopy series that follow the canopy into or out of gaps. We therefore suggest that individual treefall gaps contribute to the composition and richness of understory bird assemblages in Caribbean forests by attracting canopy dwellers rather than by attracting gap specialists. *Received 17 May 1986, accepted 6 Aug. 1986.*

Small forest openings contribute to the structural heterogeneity of tropical forests and may influence composition and richness of the bird community (Stiles 1983). In a lowland forest in Panama, Schemske and Brokaw (1981) found that gap and forest understory bird assemblages were distinct, and that several species displayed preference for either gap or forest understory. These findings are consistent with previous studies, which suggest that tropical (continental) forest birds often show narrow habitat preference (Orians 1969, Terborgh and Weske 1969, Karr and Roth 1971, Pearson 1971, Terborgh 1971). Certain species show a preference for forest openings (Willis and Oniki 1972, Stiles 1975, Gradwohl and Greenberg 1980). In mature lowland forest in Peru, forest openings contained bird species characteristic of secondary habitats (Pearson 1971). Often the bird species found in forest openings and second growth areas also are observed in the forest canopy, but not in the surrounding forest understory (Orians 1969, Pearson 1971, Greenberg 1981). Our work investigates understory bird communities of gaps, a larger forest opening, and surrounding mature rainforest on the Caribbean island of Puerto Rico.

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For a variety of reasons, we did not expect to find many, if any, gap specialists in the avifauna of Puerto Rican rainforests. One principal reason is the comparative lack of gaps in the forest. The contribution of the gap phase to habitat heterogeneity varies within and among forests according to several factors (Garwood et al. 1979), including treefall frequency, size class distribution of treefall gaps, and regeneration time from gap to maturity. These factors are likely to be very different on islands such as Puerto Rico, where severe hurricanes occur approximately once every 10 years (Wadsworth and Englerth 1959). Caribbean island rainforests are specially adapted to withstand frequent hurricanes. The canopy of island rainforests is generally more even, lower in stature, and lacking in emergent crowns, as compared with lowland forests not exposed to hurricanes (Odum 1970, Doyle 1981). This relatively unbroken canopy of island rainforests may be maintained by trees that typically remain standing after death, and decompose without producing a large gap. Thus, the relatively homogeneous physiognomy of Caribbean island rainforests provides only small and rare habitats for potential gap specialist species.

A second reason for predicting fewer gap species in Puerto Rico is that numerous studies have suggested that island bird populations have broader habitat preferences than those on the mainland (Crowell 1962, MacArthur et al. 1966, Keast 1970, Diamond 1971, Cox and Ricklefs 1977). Thus it seems unlikely that avian gap specialists would be present in the Puerto Rican rainforests because of the tendency for island birds to use a wide range of habitats, and because of the limited production of gaps.

Our work takes advantage of the relatively well-known avifauna of the El Verde rainforest in eastern Puerto Rico (MacArthur et al. 1966, Recher and Recher 1966, Recher 1970, Kepler and Kepler 1970, Reagan et al. 1982) to study the distribution of birds in the understory of closed forest, small gaps, and a larger forest opening. We addressed the following questions: (1) Do treefall gaps or forest openings have an assemblage of birds different from or more diverse than that of intact forest understory? (2) Do particular bird species exhibit preferences between forest understory, small treefall gaps, and larger forest openings? (3) Is the assemblage of birds found in small treefall gaps a subset of the assemblage found in larger forest openings? (4) How do forest openings contribute to bird diversity in tropical island forests?

## STUDY SITE

We captured birds in three habitats near the El Verde Field Station in the Caribbean National Forest in eastern Puerto Rico. The forest at El Verde has been well described (Odum and Pigeon 1970, Brown et al. 1983). It is classified as subtropical wet forest in the

Holdridge system and is a broad-leaved evergreen forest. The study site lies at an elevation of 350 m with moderately sloping topography, a permanent river to the north, and temporary streams running through the netting area. An average of 346 cm of rain falls per year with a slight dry season from December to April. During our study there was no rainfall in April or May of 1984 (vs an average of 58 cm for these two months). The dominant tree, tabonuco (*Dacryodes excelsa*) comprises as much as 35% of the forest canopy (Wadsworth 1951). Three tree strata are evident: a discontinuous upper layer at 24 m, a second continuous canopy at 20 m, and an understory. The understory is sparsely vegetated and has an open appearance due to the lack of branches to heights greater than half the height of most trees. Epiphytes, lianas, arborescent ferns, and understory palms are common.

## METHODS

Three understory habitats, defined by their foliage height profiles and area, were sampled with mist nets. Six nets (12 m length, 30-mm mesh) were placed in treefall gaps, six in second growth in a powerline opening, and six in the understory of the surrounding natural intact forest. We use Brokaw's (1982) definition of a gap as "a vertical hole in the forest extending through the canopy to within 2 m of the forest floor." Four gaps >12 m long were censused, two of which were large enough to accommodate two nets. The mean gap area was 117 m² (range = 78–168 m²). Nets were placed in the gaps to minimize visibility, but retain all of the net area within the gap. The gaps were surrounded by intact forest which had foliage height profiles similar to those of the forest understory nets. In this same area (Fig. 1), a powerline opening had been cut through the forest leaving a second growth strip 15 m wide and over 1.6 km long. Within this powerline cut, six nets were alternately placed across or parallel (in the center) to the long axis of the opening. Paired with the powerline nets were six forest understory nets set in the same compass direction as the corresponding powerline net and at least 15 m from the corresponding net and 10 from the edge of the powerline opening. Small temporary streams (dry from March through May) ran through all three habitats and under nets 3, 8, and C. Because the presence of water could influence capture rates, these nets are excluded from analysis unless specifically mentioned.

We determined foliage height profiles to quantify the vegetation surrounding the nets in each habitat, using the techniques of Karr (1971) and Schemske and Brokaw (1981). We established the six 12-m long transects parallel to each net at 0.5 m intervals on each side of the net. The presence or absence of vegetation within each of 13 height intervals was recorded at every 1 m along the transects. Height intervals (in meters) were 0–0.25, 0.25–0.50, 0.50–0.75, 0.75–1.00, 1.0–1.5, 1.5–2, 2–3, 3–5, 5–10, 10–15, 15–20, 20–25, and 25–30. To sample vegetation below 2 m, we recorded all vegetation that touched a vertical 1.5 cm × 2 m pole placed at each sampling point. For height intervals above 2 m we sighted along the vertical pole and recorded the presence or absence of vegetation in each height zone as determined by a rangefinder. For each net, we sampled at 156 points and calculated the percent cover for each height interval.

All nets were run for two days on each of 19 weekends (designated as netting sessions), at two or three-week intervals during a 12-month period from 8 October 1983 to 30 September 1984. Initially, netting was done every two weeks, but because of declining capture rates we switched to three-week intervals in December. This schedule was maintained until the end of the study, with the exception of April and May, when we returned to two-week intervals because of higher capture rates. Nets were open from dawn to dusk on both Saturday and Sunday of each netting session, and were checked every 1–2 h. The nets were closed for 7.5 h during the day on 10 June due to heavy rainfall. All captured birds were given unique color-band combinations except for hummingbirds and todies in which a combination of tail feathers were clipped.
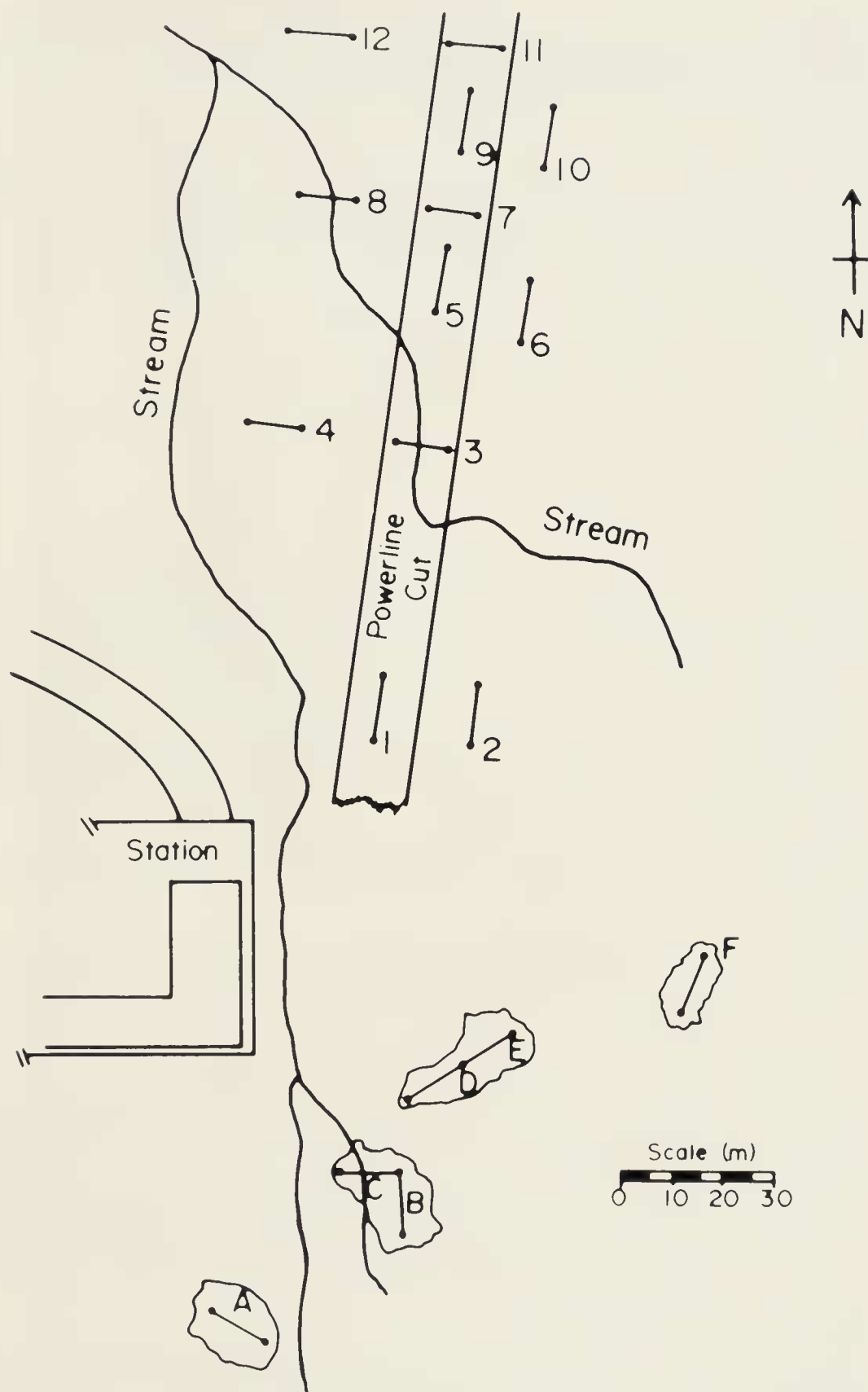
FIG. 1. Map showing the location of all nets at the El Verde research station, Puerto Rico. Treefall gap nets are shown with letters, nets in the powerline opening have odd numbers, and forest understory nets have even numbers.

A Friedman rank sums test based on distribution-free multiple comparisons (Hollander and Wolfe 1973:151) was used to compare the captures of a species among the three habitats when sample sizes were sufficient (Table 1). This test makes all possible pairwise comparisons among the three habitats while controlling for the experimentwise error rate within each species.

We used a polar ordination technique (Bray and Curtis 1957) as used by Beals (1960) and Schemske and Brokaw (1981) to examine whether the three different habitats support different assemblages of birds. With this technique, each net is considered to be a sample of the avifauna of one of the habitats. The relative similarity of the net samples can be determined by ordination of all nets with respect to bird composition. A percentage similarity (PS) matrix was used to construct the Bray-Curtis ordination:

$$PS = 100 - \tfrac{1}{2} \sum_{i=1}^{n} |P_{ai} - P_{bi}|$$

where $P_{ai}$ and $P_{bi}$ represent the percent individuals belonging to species i in samples a and b.

## RESULTS

Vegetation profiles showed considerable differences between the forest understory and gap nets (Fig. 2). While much of the vegetation in the gaps was concentrated below 2 m, vegetation in the forest was thickest at 10–15 m. Gaps and powerline openings contained numerous low woody shrubs and herbs at net height, often with the branches of a few canopy trees extending into or alongside the gap. Generally, vegetation under the powerline was higher than that of gaps, which had a more even distribution throughout the height profile. The lower vegetation of the forest understory frequently was composed of palms which were rare in both the treefall gaps and powerline opening.

In 7524 net hours we recorded 531 captures representing 17 species in 10 families (Table 1). During October through February the overall capture rates remained relatively constant at an average of 0.06 captures/net-h. The rate increased from February to April, with a peak on April 14 of 0.14 captures/net-h. After April, rates declined to a low of 0.03 captures/net-h on 20 July. Much of this seasonal pattern was attributable to captures in the forest understory nets (range 0.0–0.12 captures/net-h) and powerline opening nets (range 0.03–0.23 captures/net-h). Gap nets showed a different pattern with a maximum peak of 0.14 captures/net-h on 18 November and a low of 0.01 captures/net-h on 30 June. Overall, we averaged 27.9 captures per netting session (range = 13–59) and 5.6 species per session (range = 4–10).

Total captures differed among the three habitats (Table 1). The 163 captures in the powerline nets were significantly more ($\chi^2 = 9.458$, $P < 0.005$) than the 112 captures in the gaps, which, in turn, were significantly more ($\chi^2 = 10.215$, $P < 0.005$) than the 69 captures in the forest. Whereas

## TABLE 1
### TOTAL CAPTURES OVER ALL NETS

| Species | Number of captures[a] | | | | | | Significance level[b] | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | Powerline | | Treefall | | Forest | | | | |
| | A | B | A | B | A | B | P vs T | P vs F | T vs F |
| Bananaquit (*Coereba flaveola*) | 161 | 76 | 69 | 45 | 25 | 23 | *P* < 0.05 | *P* < 0.05 | *P* < 0.05 |
| Puerto Rican Tody (*Todus mexicanus*) | 34 | 20 | 34 | 28 | 9 | 5 | N.S. | *P* < 0.05 | *P* < 0.05 |
| Puerto Rican Emerald (*Chlorostilbon maugaeus*) | 33 | 17 | 18 | 13 | 13 | 10 | N.S. | N.S. | N.S. |
| Ruddy Quail-Dove (*Geotrygon montana*) | 21 | 20 | 9 | 8 | 23 | 19 | *P* < 0.05 | N.S. | *P* < 0.05 |
| Green Mango (*Anthracothorax viridis*) | 18 | 9 | 0 | 0 | 0 | 0 | *P* < 0.007 | *P* < 0.007 | N.S. |
| Black-whiskered Vireo (*Vireo altiloquus*) | 8 | 6 | 3 | 3 | 4 | 4 | N.S. | N.S. | N.S. |
| Black-throated Blue Warbler (*Dendroica caerulescens*) | 7 | 4 | 7 | 6 | 0 | 0 | N.S. | N.S. | *P* = 0.039 |
| Puerto Rican Bullfinch (*Loxigilla portoricensis*) | 2 | 1 | 6 | 6 | 0 | 0 | N.S. | N.S. | *P* = 0.029 |
| Puerto Rican Tanager (*Neospingus speculiferus*) | 5 | 3 | 0 | 0 | 2 | 2 | N.S. | N.S. | N.S. |
| Louisiana Waterthrush (*Seiurus motacilla*) | 2 | 2 | 0 | 0 | 4 | 2 | N.S. | N.S. | N.S. |
| Red-legged Thrush (*Turdus plumbeus*) | 2 | 2 | 1 | 1 | 1 | 1 | N.S. | N.S. | N.S. |
| Pearly-eyed Thrasher (*Margarops fuscatus*) | 1 | 1 | 1 | 1 | 1 | 1 | N.S. | N.S. | N.S. |
| Black-faced Grassquit (*Tiaris bicolor*) | 2 | 2 | 0 | 0 | 1 | 1 | N.T. | N.T. | N.T. |
| Northern Parula (*Parula americana*) | 1 | 0 | 1 | 1 | 0 | 0 | N.T. | N.T. | N.T. |
| Black-throated Green Warbler (*Dendroica virens*) | 0 | 0 | 0 | 0 | 0 | 1 | N.T. | N.T. | N.T. |
| American Redstart (*Setophaga ruticilla*) | 1 | 0 | 0 | 0 | 0 | 0 | N.T. | N.T. | N.T. |
| Black-and-white Warbler (*Mniotilta varia*) | 1 | 0 | 0 | 0 | 0 | 0 | N.T. | N.T. | N.T. |
| Total | 299 | 163 | 149 | 112 | 83 | 69 | | | |

[a] Number of captures per powerline opening, treefall gap, and forest understory nets. Captures within each habitat are divided into the totals for all nets in a habitat (A) and totals without the stream nets (B).

[b] Significance levels for Friedman rank sums tests (see text) for pairwise comparisons among the three habitats with stream nets excluded (B only). P = powerline, T = treefall gap, and F = forest understory. N.S. = *P* > 0.05; N.T. = no test.
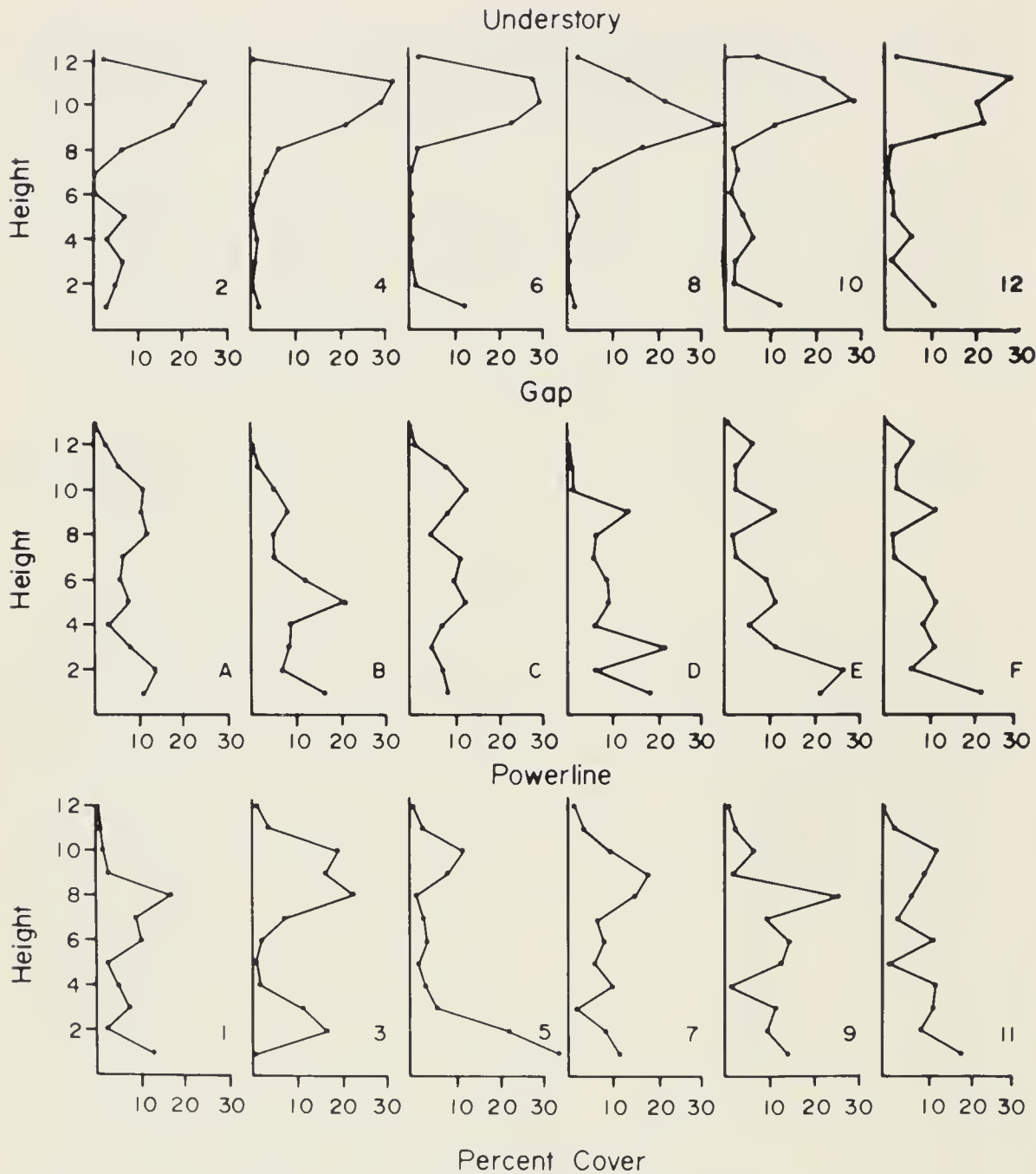
Understory

Gap

Powerline

Percent Cover

FIG. 2. Foliage height profiles for forest understory (upper), treefall gap (center), and powerline opening (lower) nets. Percent cover represents the percent of vegetation touches in a given height interval. N = 156 sample points per net. Height intervals are in meters (1 = 0–0.25, 2 = 0.25–0.50, 3 = 0.50–0.75, 4 = 0.75–1.0, 5 = 1.0–1.5, 6 = 1.5–2.0, 7 = 2–3, 8 = 3–5, 9 = 5–10, 10 = 10–15, 11 = 15–20, 12 = 20–25).

capture rates differed among the habitats, the total number of species captured in each habitat was similar (13 in powerline, 10 in gaps, 11 in forest); however, the average number of species captured per netting session differed among the habitats. This average was 4.7 species (range = 2–7) in the powerline nets, significantly greater (Mann Whitney $U = 252.5$,

$P < 0.025$) than the mean of 3.3 (range = 2–6) in the gaps, but it did not differ from the mean of 2.4 (range = 0–7) in the forest. Thus the powerline nets captured the largest number of individuals and the highest average number of species per netting session.

Using a Friedman rank sums test we found that six species (Bananaquit, Puerto Rican Tody, Ruddy Quail-Dove, Green Mango, Black-throated Blue Warbler, Puerto Rican Bullfinch) were captured more frequently in one habitat of a pair, providing evidence for habitat preference. Assuming random processes, how many species would be expected to show at least one difference among the three habitat pairs? At the 5% level of significance with three habitats, a minimum of three days in which a given species was captured is required: of the 12 species with three or more capture days, only 0.6 species (12 species × 0.05) would be expected to show differences among habitats based only on random processes. A comparison of this expected number of species (0.6) with the observed number of species with at least one significant difference among habitat pairs (6) indicates that selection among the habitats occurred far more often than expected by chance.

*Treefall gaps.*—No species was captured exclusively in treefall gaps. Four species, however (Bananaquit, Puerto Rican Tody, Black-throated Blue Warbler, Puerto Rican Bullfinch) were more frequently captured in gaps than in forest.

*Powerline opening.*—Three species (Bananaquit, Puerto Rican Tody, Green Mango) were captured more frequently in the powerline nets than in the nearby forest. Also, two of these species (Bananaquit, Green Mango) and the Ruddy Quail-Dove were captured more often along the powerline than in gaps, while three species (Puerto Rican Tody, Black-throated Blue Warbler, Puerto Rican Bullfinch) were captured in both habitats with similar frequency. One species, the Green Mango, was captured exclusively in the powerline nets.

*Forest understory.*—No species was found exclusively in the forest, and none had a higher capture rate in the forest. The quail-dove, however, had an unusual distribution in which the captures in the powerline and forest nets were very similar, but the 19 forest understory captures were significantly greater than the 8 gap captures.

*Stream nets.*—The presence of a stream (with or without water) had a significant effect on the total number of captures in both the powerline and gap nets (3 and B), but not in the forest (net 8). The powerline net placed across the small temporary stream captured 136 individuals or 45.5% of all powerline captures. This was significantly more ($\chi^2 = 288.49$, $P < 0.005$) than expected (16.7%) from equivalent captures among all 6 powerline nets. The 37 captures (24.8% of all gap net captures) from the

TABLE 2

MEAN AND STANDARD DEVIATION OF SIMILARITY INDEXES FOR PAIRS OF NETS WITH
COMPARISONS WITHIN THE SAME HABITAT AND BETWEEN DIFFERENT HABITATS IN EL VERDE

|  | Powerline | Gap | Understory |
|---|---|---|---|
| Powerline | 0.69 ± 0.08 | | |
| Gap | 0.64 ± 0.11 | 0.66 ± 0.09 | |
| Understory | 0.58 ± 0.11 | 0.50 ± 0.11 | 0.65 ± 0.08 |

gap net across the same temporary stream were also significantly more ($\chi^2 = 10.565$, $P < 0.005$) than expected, assuming equivalent captures in all 6 gap nets. The forest net across the same temporary stream, however, captured only 14 individuals, or 16.8% of forest captures, a value not different from that expected by chance alone ($\chi^2 = 0.00579$, $P > 0.10$).

The total number of species (including migrants) captured in the stream nets in each habitat was approximately 50% of the species captured in all nets in that habitat: 9 species captured in the powerline-stream net represented 56% of all species captured in powerline nets; 5 species from the gap-stream net represented 50% of the species caught in gaps; and 5 species from the forest stream net represented 45% of those captured in the forest. Thus the stream nets in the gap and powerline had higher capture rates than other nets in comparable habitat without streams, and each stream net captured about 50% of all species obtained within the habitat.

*Avian assemblages by habitat.* — The cumulative species curve combined for gap, powerline, and forest nets plateaued at 10 resident species, with 10 species in the powerline nets, 7 species in the gap nets, and 8 species in the forest. Although the addition of new species to these habitats may still occur, it is likely that it will be slow because all the species previously known from the El Verde forest understory (Recher 1970) were captured.

The mean percentage similarity (PS) for all net-pairs within habitats was significantly different from the mean PS for all net-pairs among habitats (two-tailed Mann-Whitney $U$-test, large sample approximation, $t = 3.712$, $P < 0.001$). Therefore, bird assemblages from net-pairs within the same habitat were demonstrably more similar than assemblages among habitats (Table 2), suggesting that the birds recognized differences among the three habitats.

Several different Bray-Curtis ordinations were made to compare nets in the three habitats. An ordination (Fig. 3A) with all species, including migrants, shows little overlap between gap and forest nets and little over-
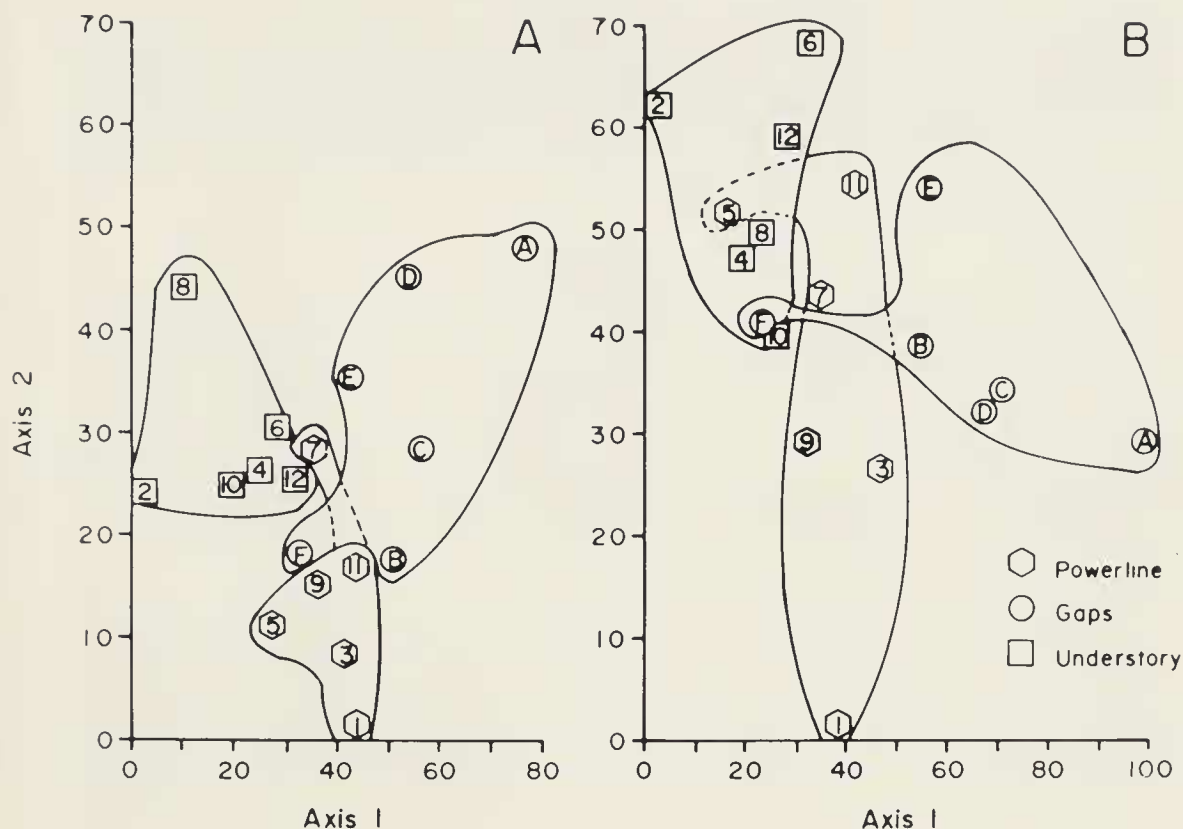
FIG. 3. Ordination of bird captures from forest understory, treefall gaps, and powerline opening nets by the method of Bray and Curtis (1957) for all species (A) and all species except the bananaquit and migrants (B). As shown in Fig. 1, each net is indicated with a number or letter.

lap between forest and powerline nets; however, the overlap of one gap net (F) with the powerline nets suggests more similarity between the two assemblages. Eliminating the migrants (this ordination is not shown) produces better separation of the forest nets from gap and powerline nets, although gap and powerline nets again overlap with net F. Because Bananaquits were the most abundant species (48% of total captures) and were captured significantly more often in powerline nets, they may influence the ordination of all other species. We eliminated this effect by running Bray-Curtis ordinations on a percentage similarity matrix calculated without Bananaquits (see Schemske and Brokaw 1981). The results of these ordinations are similar, suggesting a separation of gap and forest nets, but with some overlap of gap and powerline nets and powerline and forest nets (Fig. 3B).

From the ordinations it is difficult to determine if the presence of running water under a net affected the assemblage of birds captured. For instance, stream nets in the gap (B) and powerline (3) are as similar to each other as to the others in corresponding habitat (Fig. 3A); however,

the forest stream net (8) was very different from these nets as well as the other forest nets. When Bananaquits and migrants are eliminated from the ordination (Fig. 3B) the assemblages of birds captured in stream nets (3, 8, C) are similar to each other and to others in the corresponding habitat.

DISCUSSION

Although treefall gaps in the tabonuco forest may be too small ($\bar{x}$ = 117 m² vs 130 m² in Panama; Schemske and Brokaw 1981) and rare to support gap specialist species, certain species may spend a comparatively large amount of time in gaps. No species was unique to gaps. With the exception of the mango and bullfinch most of the species were found in all three habitats, although frequently at different abundance levels. All species with higher capture rates in gaps than in surrounding forest understory (Bananaquit, tody, bullfinch, Black-throated Blue Warbler) were also found in the canopy; the higher capture rates of bullfinches and Black-throated Blue Warblers in the gaps may be attributed to their tendency to follow the canopy down into gaps, as has been found for some species in Costa Rican rainforests (Stiles 1983). In some instances, Bananaquits and todies may be following the contour of the canopy in the reverse direction out of the gap into the canopy. Thus, it is the higher abundance of these occasional canopy species that produces the appearance of a gap assemblage different from that of the surrounding tabonuco forest understory. This contrasts with the studies of Schemske and Brokaw (1981) in lowland forest in Panama, where they concluded that differences between gap and forest understory assemblages reflected true habitat preferences of understory birds, rather than a tendency for birds to follow the canopy into gaps.

While the relative abundance of canopy and understory species may affect the composition of the assemblage of species in each understory habitat, the number of resident species from the canopy, understory, or both height zones is nearly identical in each of the three habitats (Table 3). Adding migrants to this analysis substantially increases the number of canopy species in the powerline opening (7 species, 44% of all powerline species) and treefall gap (6, 55%), but not the forest understory (2, 18%). This is because migrants are primarly leaf-gleaning insectivores foraging on sunlit foliage of its height above the ground. The only exception to this was the Louisiana Waterthrush, found in the understory, and usually near streams.

Our findings differ from those of Schemske and Brokaw (1981), who found that although the numbers of individuals captured in gaps and nearby understory were similar, more species were captured in gaps. They attrib-

TABLE 3

SPECIES CAPTURED IN THE THREE HABITATS AND THEIR DISTRIBUTION IN THE FOREST
CANOPY OR UNDERSTORY (FOR EACH HABITAT, THE SPECIES ARE SEPARATED INTO
RESIDENT SPECIES ONLY AND ALL SPECIES, INCLUDING MIGRANTS)

| Habitat | Foraging height[a] | | |
|---|---|---|---|
| | Canopy only | Understory only | Canopy and understory |
| Powerline | | | |
| Residents only | 2 (20)[b] | 4 (40) | 4 (40) |
| All species | 7 (44) | 5 (31) | 4 (25) |
| Treefall | | | |
| Residents only | 2 (29) | 3 (42) | 2 (29) |
| All species | 6 (55) | 3 (27) | 2 (18) |
| Forest | | | |
| Residents only | 1 (13) | 4 (50) | 3 (37) |
| All species | 2 (20) | 4 (40) | 4 (40) |

[a] Classification of the foraging zone for El Verde birds is based on observations of Waide in Reagan et al. (1982), and Wunderle (unpubl. data).
[b] Percentage of row total.

uted the higher number of species in gaps to the more heterogeneous
"edge" habitat of the gap which provides a diversity of foraging oppor-
tunities (Terborgh 1977), and to greater foliage density and its higher
productivity (Halle et al. 1978) at net height in the gaps rather than high
in the canopy (Karr and Roth 1971, Willson 1974).

It is possible that an "edge effect" influenced captures in the forest nets,
which were located 10 m from the powerline opening. To examine this
possibility we compared our results with those of Waide (in Reagan 1982)
who sampled understory birds for 3–4 days using 10–11 nets at three sites
in old undisturbed forest at El Verde. Overall, our forest capture rates
were 0.055 captures/net (range = 0–0.12 net/h) similar to his value of
0.063 (range = 0.04–0.09 net/h). Comparing the total captures for the 8
most common species, we did find a significant difference between our
forest sites and those of Waide (row × column test of independence, $G = 29.27$, $P < 0.005$). However, our higher Bananaquit captures account for
this difference, because analysis without Bananaquits indicates no signif-
icant difference for the remaining seven species ($G = 8.39$, $P > 0.1$). Thus,
our high Bananaquit captures in the forest may have resulted from an
edge effect. As the edge effect was not apparent for the other forest species,
the ordination without Bananaquits (Fig. 3B) probably best illustrates the
forest understory assemblage.

In the tabonuco forest, the gap assemblage appears to be a subset of the assemblage of larger forest openings, represented here by the powerline opening. The mean paired similarity index for gap and powerline was highest of all habitat pairs (Table 2), and when species are ranked by abundance in the gaps and powerline opening, the sequence is the same for the first four species (Bananaquit, tody, emerald hummingbird, quail-dove). Thus the gap assemblage is a subset of the powerline opening (they share 10 species). Comparison of the powerline opening assemblage with even larger second growth openings of similar foliage profile suggests that the abundance of canopy dwelling species, such as the Red-legged Thrush, Pearly-eyed Thrasher, Puerto Rican Tanager, Puerto Rican Lizard-Cuckoo (*Saurothera vieilloti*), Blue-hooded Euphonia (*Euphonia musica*), and Stripe-headed Tanager (*Spindalis zena*) increases with second growth patch size (Wunderle, unpubl. data).

The size of our second growth patches (gaps and powerline opening) was not great enough to discourage forest understory species, which regularly wandered into both gaps and the powerline opening. Only one species, the Ruddy Quail-Dove, can be considered to be primarily restricted to the forest understory in Puerto Rico (Raffaele 1983). Yet this species showed an equal number of captures in the forest and powerline nets and significantly fewer captures in the gaps. Although the distribution of food supply may partially explain this distribution, other factors such as patch size and geometry and the presence of thick understory vegetation may be important.

The distribution of individual species might best be explained in terms of food distribution, which is probably related to vegetation. For those species gleaning insects from the foliage (todies, Bananaquits, Black-throated Blue Warblers, and other warbler species) the gap and powerline opening had the highest density of foraging substrate at net level, and thus more captures of canopy species than in the forest understory nets. Another foliage gleaner, the Black-whiskered Vireo, was captured in forest understory nets only during early April, at a time when vireo territories were being set-up. Similarly, nectarivore distribution can be directly related to flower distribution. For example, the Puerto Rican Emerald was found in all habitats, as were the flowers with short corollas (e.g., *Palicourea crocea*) from which they fed; the Green Mango, which fed exclusively from *Heliconia* flowers, was found only in the powerline opening, the only location of this food source—and the only understory habitat with long-tubed flowers. Mango populations fluctuate with the availability of long-tubed flowers (Kodric-Brown et al. 1984) and will move into any habitat where these flowers are available.

During this study, the rate of understory fruit production was low, although it appeared to be highest in the forest openings, as found in temperate forests (Thompson and Willson 1978) and lowland tropical forest in Costa Rica (Levey, pers. comm.). Thus, higher concentrations of fruit-eating birds in gaps may be a direct result of higher concentrations of fruiting plants in gaps (Willson et al. 1982; Blake and Hoppes 1986; Martin and Karr, in press). Quail-doves are known to congregate under fruiting canopy trees such as *Dacryodes excelsa* and *Sloanea berteriana* (Recher 1970), which are found along the powerline and near the forest understory nets, but are absent along the treefall gaps; this may contribute to their unusual distribution in this study. Similarly, the frugivorous bullfinch was most commonly encountered in treefall gaps, where it fed on the fruits of *Urera baccifera*. This plant was common in gaps, less common in the powerline opening, and absent from forest understory. Fruit abundance in gaps, however, was probably insufficient to attract other canopy frugivores such as the Stripe-headed Tanager, Puerto Rican Tanager, and Blue-hooded Euphonia to the study area.

Karr and Freemark (1983) found that microclimate factors such as moisture gradients influenced bird distributions in tropical forest undergrowth in a complex manner, varying in both space and time. While they did not have food supply data, their data suggested that birds might track microclimatic variables for physiological reasons. In El Verde, running water may attract birds within the more open habitats. Even when water was not present in the temporary streams, the stream nets in the gap and powerline opening still had high capture rates. In fact, the highest seasonal capture rates occurred in the powerline stream net during April when water was not present. It is possible that many canopy species were coming down into gaps in search of water or at least more humid microclimates. Whether food (insects) is more abundant near temporary streams is unknown. Whatever the cause, the presence of a temporary stream appears to make forest openings even more attractive to birds in the tabonuco forest.

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